WEALDEN MAMMALIAN FOSSILS

by WILLIAM A. CLEMENS

ABSTRACT. Only two of the previous identifications of specimens considered to be teeth of Wealden mammals can be accepted without reservation. A special collecting technique including both chemical and mechanical processes facilitated the discovery of eight more Wealden mammalian fossils. Five were found in the Cliff End Bone Bed, a part of the Ashdown Beds, and the remainder in the Paddockhurst Bone Bed, a part of the Grinstead Clay. These fossils give additional information about the morphology of the multituberculate *Loxaulax valdensis* and demonstrate the presence of a symmetrodont and eupantothere in England in the early (pre-Aptian) Cretaceous.

THE fossil record of Mesozoic mammals is limited. Large collections of mammalian fossils of late Jurassic age have been made in the Purbeck Beds of England and the Morrison Formation of the United States. The Albian mammalian fauna is known from fossils found in the Trinity Sand of Texas. The only record of mammals that certainly lived in the interim between the Purbeckian and Albian consists of the rare specimens discovered in the Wealden of England. Two mammals found in the Husin Series of Manchuria also may be of post-Purbeckian and pre-Albian age, but the correlation of the strata in which they were found is still open to question (see Patterson 1956, pp. 30–31). The first specimen considered to be a mammalian fossil discovered in the Wealden of England was described in 1891; in the two following decades four more specimens were found. After this initial activity almost fifty years elapsed before another Wealden mammalian fossil was discovered. In the autumn of 1960, working under the auspices of a National Science Foundation Postdoctoral Fellowship, I began a survey of British Mesozoic mammals and the localities at which they were found. At the suggestion of Dr. K. A. Kermack, one of the first localities visited was Cliff End, where three of the Wealden mammalian fossils had been found in a bone bed cropping out on the shore. Blocks of the bone bed found scattered along the beach proved to contain mammalian fossils. As word of my interest in Wealden mammals spread, I was told of another promising bone bed in Paddockhurst Park that also proved to contain isolated mammalian teeth. Some of these fossils were exhibited at a meeting of the Geological Society (Clemens 1960). This paper is an interim report on a research project that is being continued under the direction of Dr. K. A. Kermack of the Department of Zoology, University College, London.

All catalogue numbers cited are from the British Museum (Natural History) Catalogue of Fossil Mammalia.

PREVIOUS INVESTIGATIONS

In 1891 A. Smith Woodward announced the discovery of a tooth of a Wealden mammal. Two years later Richard Lydekker described another specimen and in 1911 Woodward reported on three more. Study of these fossils and the circumstances of their discovery has brought to light facts confirming the unpublished suggestions of several palaeontologists that the identification of some of the fossils as teeth of Wealden

mammals is incorrect. The first fossil thought to be a Wealden mammalian tooth (M13134) was found by Charles Dawson in a bone bed within the Wadhurst Clay exposed in the 'Old Roar Quarry' near Hastings. It was an isolated tooth having both the heavily worn crown and root preserved. Later it was damaged and all that remains is a fragment of the root. Woodward (1891, p. 586) described the crown of the tooth as being '. . . supported by two roots, which are robust, of nearly equal size and depth, incompletely separated in the upper half and terminating obtusely'. Loss of parts of the tooth has revealed that, although deeply grooved on the surface, the root contains a single pulp cavity rather than two as would be expected if this structure were two incompletely separated roots.

After comparing this Wealden tooth (M13134) with haramiyid teeth and the M_2 of *Ctenacodon* (*Plagiaulax*) *minor*, Woodward tentatively identified it as the molar of a multituberculate and allocated it to the genus *Plagiaulax* under the provisional name *P. dawsoni*. The similarities on which this identification was based are neither numerous, detailed, nor fully convincing. Simpson (1928, p. 52) commented that the tooth '. . . is probably Plagiaulacid, although its generic and specific affinities are quite undeterminable'. The presence of a single pulp cavity in the root reduces the probability that the tooth is a plagiaulacid molar, which has two roots, and strongly suggests that it is not the tooth of a mammal.

In 1893 Lydekker identified another fossil (M5691) as an incisor of a Wealden multituberculate. In the discussion following the presentation of Lydekker's paper at the Geological Society, Sir John Evans recounted the history of the discovery of the tooth: 'He [Evans] found it at Hastings, in a block of Tilgate Grit which formed part of a heap by the side of the sea-shore, and almost immediately afterwards gave it to Prof. Prestwich, in whose collection it was mislaid for a period of over thirty years. On again coming across it, Prof. Prestwich placed it at the disposal of the speaker . . .' (Lydekker 1893, p. 283). In the course of the same discussion, Dawson stated: '. . . it was unfortunate that the specimen had been taken from a loose block, because at Hastings stones foreign to the district and miscellaneous drifted stones from the shore were frequently broken up for road-metal. From the limited view permitted him of the specimen that evening he was unable to identify the matrix as from the Hastings district; and he did not recognize the fragmentary specimen before them as a portion of a mammalian tooth.'

Dawson appears to have been alone in questioning the identification of this fossil as a mammalian tooth. Study of the specimen substantiates Lydekker's observation that there is no way of distinguishing it from a rodent incisor. Because it was and still is thought to be unlikely that the Rodentia had evolved as a discrete group in the Early Cretaceous and, because multituberculates possessed somewhat rodent-like incisors, Lydekker and others concluded that this tooth was probably a multituberculate incisor. Excluding the specimen in question, the available fossil record of multituberculates demonstrates that incisors closely resembling those of rodents were evolved only in one Tertiary subfamily, the Eucosmodontinae. The convergence was far from complete and isolated incisors of these and other multituberculates can be distinguished from the incisors of rodents (Jepsen 1937). On the basis of the size, curvature, and cross-section of the crown and the distribution of enamel, the tooth described by Lydekker can be identified as an incisor of a rodent. The only attribute of the fossil that precludes this identification is its supposed stratigraphic provenance. The fossil was preserved in a

block of stone picked up on the shore. Its stratigraphic provenance was determined through identification of the enclosing sediment as 'Tilgate Grit', a name once applied to calcareous sandstones now known to be present at various levels within the Hastings Beds. This identification was challenged by Dawson and later Simpson (1928, p. 192) commented: 'The specimen, moreover, is not in such a sandstone [Tilgate Grit] but in a very crumbly clay, so that its exact level must be considered very dubious.'

To the best of my knowledge no teeth closely resembling the fossil described by Lydekker have been found *in situ* in English Wealden strata. The tooth from Hastings is similar in morphology and, superficially at least, in mode of preservation to upper incisors of *Theridomys sp.* found in argillaceous, Tertiary strata cropping out on the Isle of Wight and adjacent parts of the mainland. The nearest outcrops of these strata are over 70 miles away from Hastings. Similar incisors of rodents also have been found in Tertiary strata of the London basin that extend to within approximately 35 miles of Hastings. Dawson was first to suggest that the fossiliferous block might not have come from the Wealden cropping out near Hastings but might have been introduced from some other area. Although well removed from the Hastings district, the Tertiary strata of the Hampshire and London basins are not so distant as to preclude all possibility of the specimen being accidentally introduced from either area.

In summary, if an identification were based on dental morphology alone the tooth in question would be identified as a rodent incisor. The only controverting evidence is the supposed stratigraphic provenance of the fossil. The identification of the enclosing sediment as Tilgate Grit is incorrect, and there is no unequivocal evidence to support the former assignment to the Early Cretaceous. The block containing the fossil possibly was a fragment of a Tertiary stratum drifted on to the beach at Hastings or accidentally introduced during road construction. Although final judgement should be reserved until our knowledge of the morphology of Wealden multituberculates is more complete, the available evidence suggests that the fossil (M5691) probably is the incisor of a Tertiary rodent rather than a Wealden multituberculate.

In 1911 Woodward described three more specimens that had been discovered at Cliff End by P. Teilhard de Chardin and F. Pelletier, who were assisting Dawson. Two of these fossils are multituberculate teeth. One of them (M10480), the type of *Loxaulax valdensis* Simpson, had been described in detail by Woodward (1911, pp. 278–9) and Simpson (1928, pp. 49–50). The second (M10481) is probably a fragment of an M² of a member of the same species. Both teeth are still imbedded in sediment that is lithologically similar to the blocks of Cliff End Bone Bed found by our field parties. The third tooth was described by Woodward (1911, p. 278) as follows: '. . . most of the crown has decayed, but the two divergent roots are well displayed, the one somewhat stouter than the other'. This fossil was not recorded in the British Museum (Natural History) Catalogue of Fossil Mammalia in 1912 when the other two teeth from Cliff End were assigned specimen numbers. Recently a specimen was found in the collection with the following label: 'Mammal tooth, Fairlight, Ashdown Sand, N. Hastings, C. Dawson 15/1/1911.' This fossil, now catalogued as M20241, agrees with Woodward's brief description and probably is one of the fossils discovered by Teilhard de Chardin and Pelletier. The crown is almost completely destroyed; only a small band of enamel or enamel-like substance remains. The coronal dimensions are: length = 3·1 mm., width > 1·2 mm. The root consists of a large, cylindrical, grooved body approximately 1·8 mm.

long that terminates in two divergent branches, the largest of which is approximately 1·1 mm. long. Even though the root is bifid apically it does not resemble the roots of Late Jurassic or Early Cretaceous mammalian teeth. Also the teeth of these mammals are, for the most part, smaller than M20241. The mammalian affinities, if any, of this tooth will have to be regarded as indeterminable.

Thus of the fossils collected in and prior to 1911 only M10480 and M10481 remain as unquestionable Wealden mammalian teeth. The mammalian affinities of two of the other fossils, M13134 and M20241, are doubtful, and the tooth described by Lydekker, M5691, probably was not part of the dentition of a Wealden multituberculate. After 1911 no more Wealden mammalian fossils were discovered until 1960; but interest in the stratigraphy and the fauna of the Wealden did not decline. Of the studies carried on after 1911, the work of P. Allen, especially his reports on the stratigraphy (Allen 1959) and a study of Wealden bone beds (Allen 1949), and Simpson's (1928) review of Wealden mammals, are especially pertinent.

## DESCRIPTIONS OF THE LOCALITIES AND THE MAMMALIAN FOSSILS

Grid coordinates given in the locality descriptions are those of the National Grid and lie in the 100-kilometre square 51 (TQ).

(1) CLIFF END BONE BED

Location and collecting technique. The exact locality where Teilhard de Chardin and Pelletier collected was not described in detail by Woodward (1911). Many years later Allen, using a description of the site obtained from Woodward in 1938, relocated the bone bed and published a locality description (Allen 1960*a*, p. 11) in which he stated: '. . . rapid erosion of the cliffs has re-exposed the celebrated bone-bed . . .'. On our collecting trips in the autumn of 1960 and the following spring an outcrop of the bone bed could not be found; apparently the forces of erosion had destroyed or covered what they once revealed. Loose blocks of bone bed containing the new mammalian fossils were, however, collected from the wave-cut platform and the shingle; most were found within 100 yards of the foot of the cliff. These blocks ranged in size from cobbles to a fragment of the stratum nearly 4 feet in diameter and were distributed over an area (text-fig. 1) extending northward from a point approximately 2,000 feet north-east of Haddock's Cottages (88751280) to a point near the northern end of the cliff (88851305). Because no bone beds could be found cropping out in the area, it is assumed that all the loose blocks were derived from the intermittently exposed Cliff End Bone Bed described by Allen.

The Cliff End Bone Bed is a thin stratum composed of the comminuted bones and teeth of fish, amphibians, reptiles, and, very rarely, mammals concentrated in a hard, calcareous, coarse sandstone. The stratum, part of the Ashdown Beds, is never more than 4 or 5 inches thick, and its upper surface is ripple-marked. In order to find the minute mammalian fossils a large quantity of rock, 2 or 3 hundredweights, had to be processed. After some experiment the following technique was found to be most efficient: The calcareous cement was dissolved with dilute formic acid (a 10 to 20 per cent. solution). The material that remained was washed and dried and then passed through a set of graded sieves. The coarser fraction, material caught in 12-mesh and coarser sieves, was sorted without further treatment. The finer fraction was placed in a mixture of bromo-

form or tetrabromethane and dibromethane to give the density required to separate the quartz from the residue of fossils and heavy minerals. This residue was then washed and sorted. Separating the quartz was of particular importance because it greatly reduced the volume of fine fraction that had to be sorted under a microscope.
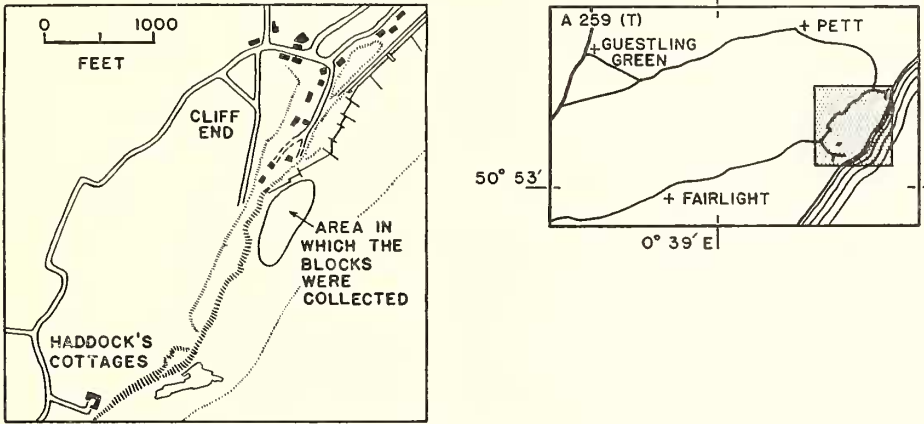

TEXT-FIG. 1. Cliff End Bone Bed, locality map. Area depicted in map on left shaded in the index map on right.

Mammalian fauna. The only fossils in earlier collections that remain as unquestionable teeth of Wealden mammals are the two multituberculate teeth found at Cliff End. One fossil, M10480, is the type specimen of *Loxaulax valdensis*; the other, M10481, is also a fragment of a multituberculate molar identified as '? *Loxaulax* sp.' by Simpson (1928). To date five more mammalian fossils have been discovered in blocks of the Cliff End Bone Bed.

Subclass ALLOTHERIA Marsh 1880
Order MULTITUBERCULATA Cope 1884
Family PLAGIAULACIDAE Gill 1872
Genus LOXAULAX Simpson 1928

Loxaulax valdensis (Woodward 1911)

Specimen M21098 (text-fig. 2). The presence of a small expansion of the crown lateral to the two rows of cusps, the morphology of the cusps, and the morphology and proportions of the crown (length = 2·4 mm., width = 1·9 mm.) indicate that M21098 is probably a right M^2. The first (anterior) and second lingual cusps are demarcated by a shallow groove, a deeper indentation separates the second and third, and the third and fourth are separated by a deep cleft. The first, second, and third lingual and two labial cusps are of approximately equal height; the fourth lingual cusp is lower. Both the posterior lingual and posterior labial cusps are slightly selenodont with the flatter face anterior. The anterior edge of the crown is concave to allow M^2 to abut against the posterolingual corner of M^1.
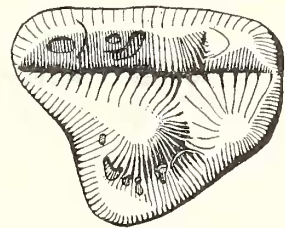
TEXT-FIG. 2. *Loxaulax valdensis* Simpson, right M^2, M21098, ×15. Occlusal view.

On the labial side of the anterior labial cusp there are several irregular, enamel-lined pits that do not appear to be the result of abrasion during mastication or post-mortem damage. The occlusal surface of the labial expansion of the crown slopes gradually from the anterior labial cusp to the edge of the crown; it is smooth and there is no evidence of a cusp or ridge.

Although the molars of plagiaulacids have only two main rows of cusps, in some species, for example, *Bolodon osborni*, the upper molars also have small expansions of the crown or cuspules in the areas in which a third cusp row is present on ptilodontid or taeniolabidid molars. Another character of the plagiaulacids is that the lengths of the molars of an individual are approximately equal while in members of the other families the first molars tend to be longer than the second. Simpson (1928, p. 49) tentatively identified the type specimen of *Loxaulax valdensis* as a left M_1. M21098 is only 0·4 mm. longer than the type specimen. Although not so pronounced as in the type, its posterior cusps are vaguely selenodont. The labial expansion of the crown appears to be relatively larger than that found on the M^2's of Purbeck multituberculates. In contrast the posterior cusps of the M^2 of *B. osborni*, which is smaller, have a more distinctly seleno-dont shape than those of M21098. Because M21098 is approximately the same length as the type of *L. valdensis*, because some of the cusps of both teeth are slightly selenodont, and because there is at present no evidence demonstrating the presence of more than one species of multituberculate in the Cliff End fauna, M21098 is provisionally allocated to *L. valdensis*. Future collections will no doubt yield evidence of other multituberculates. However, for the purposes of this preliminary report the best procedure is to refrain from the introduction of species on the probability that they will be validated by subsequent discoveries.

A comparison of M21098 with M10481, a fragment of a molar identified as '? *Loxaulax* sp.' by Simpson (1928, p. 50), suggests that the orientation of the fragment proposed by Simpson is not correct. If M10481 be regarded as a fragment of the posterior end of an M^2, then a number of resemblances to M21098 are apparent. The cusps of M10481 that Simpson thought might correspond to the 'antero-external' cusps of the type specimen are comparable to the posterior lingual cusps of M21098. The labial side of the base of the anterior labial cusp of M10481, using the orientation proposed here, is slightly enlarged, suggesting the presence of a labial expansion similar to that of M21098. The preserved cusps of M10481 differ from their counterparts on M21098 in that the posterior lingual cusp is as high as, but not so well separated from, the penultimate lingual cusp. Differences of this kind have been found in large samples of the molars of ptilodont multituberculates and cannot be accorded great significance.

Specimen M21099 (text-fig. 3). This tooth is a plagiaulacid, anterior upper premolar, that is, P^1, P^2, or P^3. The bulbous crown is surmounted by three main cusps and a small cuspule that is little more than a ridge on the surface of the enamel. Coronal dimensions are: length = 1·4 mm., width = 1·2 mm. There are two distinct but not divergent roots. M21099 closely resembles the P^3 of *Bolodon osborni*, which has three main cusps and an anterolabial cuspule.

Specimen M21106 (text-fig. 4). There are four main cusps on the crown of this anterior upper premolar. Two of them, probably the lingual cusps, are higher than their lateral

counterparts. The labial cusps are of different size; judging from the morphology of other multituberculate premolars the smaller cusp can be identified tentatively as the antero-labial cusp. There is a small cuspule anterior to the anterolingual cusp and another cuspule posterior to the posterolabial cusp. The crown is 0·9 mm. long and 0·8 mm. wide and was supported by two roots.
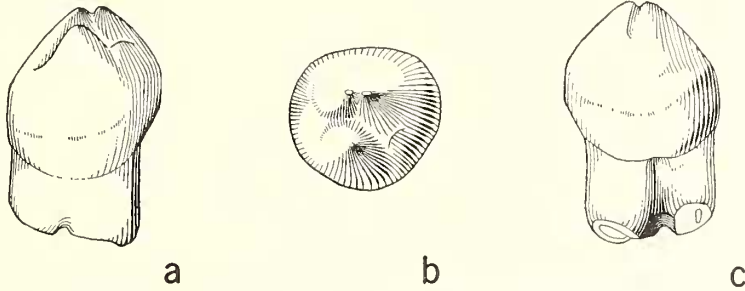
TEXT-FIG. 3. *Loxaulax valdensis* Simpson, anterior upper premolar, probably a left premolar, M21099, ×15. *a*, Labial view; *b*, occlusal view; *c*, lingual view.
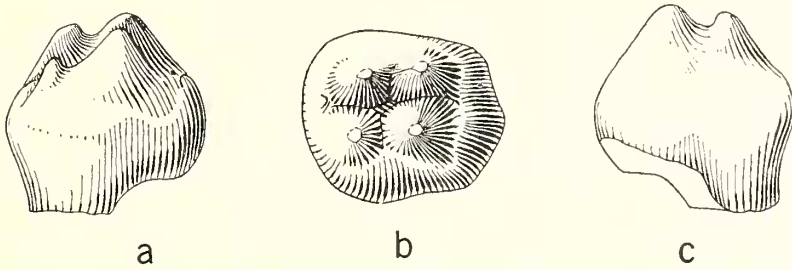
TEXT-FIG. 4. *Loxaulax valdensis* Simpson, anterior upper premolar, probably a right premolar, M21106, ×30. *a*, Labial view; *b*, occlusal view; *c*, lingual view.

Most of the anterior upper premolars of Jurassic plagiaulacids have three main cusps. The P³ of *Bolodon osborni* that has a small fourth cusp or cuspule and the P³ of *Psalodon potens* could be considered exceptions. The anterior upper premolars of ptilodontids have, in many species, a more complex cuspation. M21106, which has four main cusps, is more closely comparable to anterior upper premolars of certain Late Cretaceous ptilodontids. Probably M21106 is not a P⁴ or P⁵, because in Jurassic plagiaulacids these teeth are proportionately longer relative to width and have more than four cusps. It can be suggested that M21099, which is the larger and has a simpler crown, is a P¹ or P², and M21106 is a P² or P³. Both teeth are of the size that would be expected for premolars of *Loxaulax valdensis* and are provisionally allocated to this species. If these identifications are correct the premolar dentition of *L. valdensis* is slightly more ptilodont-like than those of the Jurassic plagiaulacids.

Specimen M21100 (text-fig. 5). One side of the crown of this single-rooted incisiform tooth is smooth and convex; the other is divided into three concave facets. There are

three small cuspules at the base of the medial facet. None of the incisors preserved in

TEXT-FIG. 5. *Loxaulax valdensis* Simpson, probably an upper incisor, M21100, ×7·5. *a* and *b*, Lateral views.

English Jurassic mammalian fossils closely resembles this tooth. The lower incisors of *Trioracodon ferox* and *Spalacotherium tricuspidens* are grossly similar but the concave sides of their crowns are not subdivided and basal cuspules are not present. Closer resemblances can be found to the I² of the American Jurassic plagiaulacid *Psalodon fortis*, and the upper incisors of some Late Cretaceous and early Tertiary ptilodontids. Therefore M21100 is provisionally identified as an upper incisor

of a multituberculate and allocated to *Loxaulax valdensis*.

Subclass THERIA Parker and Haswell 1897
Infraclass PANTOTHERIA Simpson 1929
Order EUPANTOTHERIA Kermack and Mussett 1958
Family DRYOLESTIDAE Marsh 1879
Genus cf. MELANODON Simpson 1927

cf. *Melanodon goodrichi* Simpson 1929

Specimen M21101 (text-fig. 6). The fossil consists of the lingual part of the crown and part of the lingual root of an upper molar of a eupantothere. The lingual cusp is high and from its slope three prominent, heavily worn ridges extend labiad. Even though the
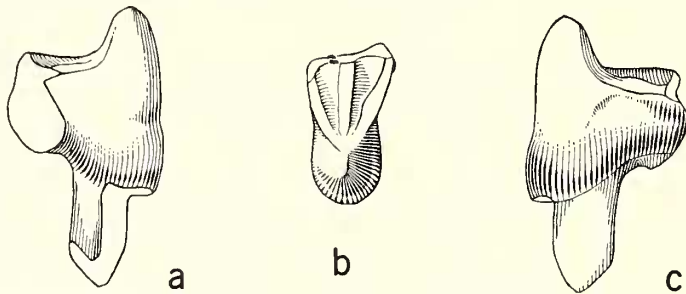

TEXT-FIG. 6. Cf. *Melanodon goodrichi* Simpson, fragment of an upper molar, M21101, ×15. *a*, Mesial view; *b*, occlusal view; *c*, distal view.

specimen suffered post-mortem abrasion, the facets on the ridges are so distinct that they must have been well developed prior to the death of the individual. One of the lateral facets is slightly expanded suggesting the presence of a small cusp.

The Cliff End fossil differs from the molars of the species of *Amblotherium* in the presence of a large, distinct, median transverse ridge; a structure not present on the molars of *A. pusillum* and small on *A. nanum* molars. The median transverse ridges on molars of *Kurtodon pusillus* are larger and more distinct than those on the molars of *A. nanum*, but not so prominent as their counterpart on M21101. Also neither of the

lateral transverse ridges on the molars of *K. pusillus* have an expansion similar to that found on one of the lateral transverse ridges of M21101. As far as can be determined from the illustrations, M21101 is closely comparable to molars of *Melanodon goodrichi* from the American Morrison Formation (Simpson 1929, pl. xv, figs. 1, 2). The molars of the type specimen of *M. goodrichi* have three distinct transverse ridges, there is an expansion of the posterior transverse ridge immediately labial to the lingual cusp, and the transverse ridges appear to have wear facets along their crests. Although not to be construed as a positive or even provisional identification, on the basis of the few available characters the comparison with *M. goodrichi* appears to be close.
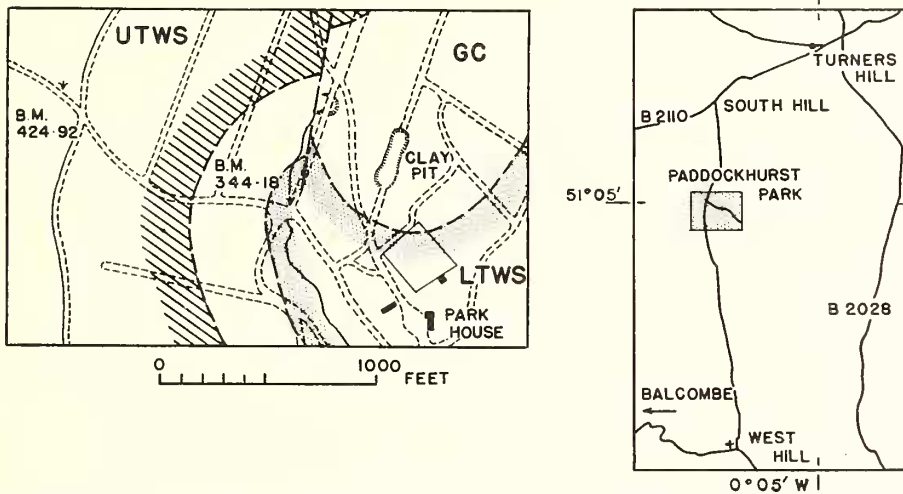
TEXT-FIG. 7. Paddockhurst Bone Bed, locality map. Area depicted in map on left shaded on the index map on right. Geologic details taken from a hitherto unpublished map by Professor J. H. Taylor. Abbreviations: UTWS, Upper Tunbridge Wells Sand; GC, Grinstead Clay; LTWS, Lower Tunbridge Wells Sand.

(2) PADDOCKHURST BONE BED

Location and collecting technique. This bone bed was discovered by Professor J. H. Taylor in the course of mapping the geology of Paddockhurst Park. The fossiliferous stratum cropped out in a now abandoned clay pit (53281334) near a park house south-west of Turners Hill (text-fig. 7). The bone bed, which is part of the Grinstead Clay, is a grey, shell-rich limestone. The vertebrate fossils concentrated in it are comminuted but are not so fragmentary or heavily abraded as those found in the Cliff End Bone Bed. During the autumn of 1960 Kermack and I were fortunate to receive several samples of the bone bed. In January 1961 with the help of Professor Taylor, Dr. Cox, and Miss Lees we collected all the fragments of the bone bed that were still visible. Further collecting will involve a large amount of preliminary work for in addition to slumping of the pit walls and the presence of luxuriant undergrowth, a number of trees have blown over and toppled into and across the pit.

The process used to free the vertebrate fossils from the rock is similar to that applied to the Cliff End Bone Bed. After the rock had been treated with dilute formic acid, usually all that remained with the fossils was a small residue of clay and ferruginous material.

Some of the residual clay could be broken down by thoroughly washing and drying the material left after the acid treatment and then placing it in a hydrogen peroxide solution (30 vol.). On completion of the chemical treatment the fossils and other residual materials were passed through a graded set of sieves. The finer fractions were sorted with the aid of a binocular microscope.

Mammalian fauna. To the best of my knowledge the specimens described below are the only mammalian fossils discovered in the Paddockhurst Bone Bed.

? Subclass ALLOTHERIA Marsh 1880

Specimen M21102 (text-fig. 8). The crushed root is long and appears to have been of approximately the same diameter throughout its length, but it may have been con-

TEXT-FIG. 8. ? Allotherian, incisor, M21102, ×9. Lateral view.

stricted apically. One side of the crown is a shallow, concave basin that is subdivided by a low, longitudinal ridge; the other side (shown in text-fig. 8) is convex and smooth. The tip of the crown has been blunted by wear and the eminence behind the apex may be the base of a cusp. Among the Mesozoic mammals only the multituberculates are known to have had large, long, somewhat gliriform incisors; therefore M21102 is allocated with a query to the Subclass Allotheria.

Subclass THERIA Parker and Haswell 1897
Infraclass PANTOTHERIA Simpson 1929
Order SYMMETRODONTA Simpson 1925
Family SPALACOTHERIIDAE Marsh 1887
Genus cf. SPALACOTHERIUM Owen 1854

cf. *Spalacotherium tricuspidens* Owen 1854

Specimen M21103 (text-fig. 9). The paraconid and metaconid of this left lower molar are close to the base of the protoconid, separated from it by shallow grooves. The basal cingulum encircles the crown, and a small anterior and a slightly larger, posterior cingular cusp are present. On the posterolabial side of the crown there are two indentations in the cingulum; probably the lingual indentation received the anterior end of the following molar. The convex lingual side of the crown is higher than the labial; the dimensions of the crown are: length = 0·80 mm., width = 0·55 mm.

The acute angle formed by the trigonid cusps and the presence of a continuous lingual cingulum indicate that M21103 is a molar of a spalacotheriid symmetrodont. Five genera have been allocated to this family: the Late Jurassic *Spalacotherium*, *Tinodon*, *Eurylambda*, and *Peralestes* (based on an upper dentition and probably a synonym of *Spalacotherium*) and the Early Cretaceous *Spalacotheroides*. The molars of *Tinodon* differ from M21103 in their wide-angled trigonid and the absence of a labial cingulum. Among the presently known genera of spalacotheriids, *Eurylambda*, known only from an upper molar, probably is most closely related to *Tinodon*. Allocation of these two genera to the Spalacotheriidae, the family to which M21103 certainly pertains, has been

questioned recently by Patterson (1956, p. 87). M21103 is more closely comparable to the molar of *Spalacotheroides*, but it differs in several important characters. The angle formed by the trigonid cusps of the *Spalacotheroides* molar is more acute, the crown is shorter relative to its width, and the basal cingulum is not continuous around the protoconid. M21103 is smaller than any of the molars that have been referred to *Spalacotherium tricuspidens*, but otherwise it resembles any of the anterior molars of this species. The posterior molars of *S. tricuspidens*, particularly M_7, differ from the more anterior molars in the smaller size of the protoconid and greater separation of the cusps of the
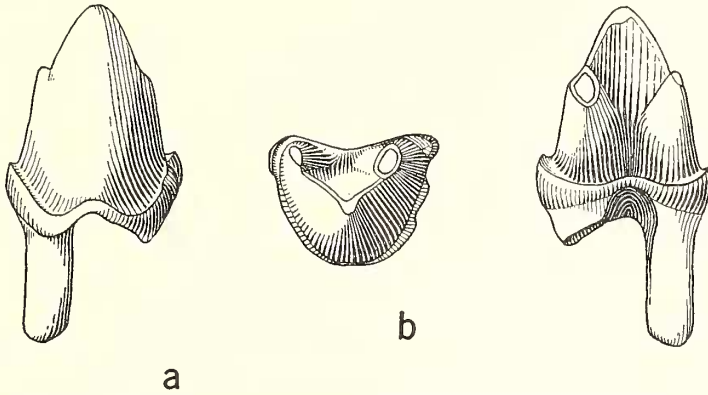
TEXT-FIG. 9. Cf. *Spalacotherium tricuspidens* Owen, left lower molar, M21103, ×30. *a*, Labial view; *b*, occlusal view; *c*, lingual view.

trigonid. The length of an anterior molar, M_1 to M_5, of *S. tricuspidens* ranges from 1·6 mm. to 1·8 mm. If M21103 is correctly identified as an anterior molar its smaller size (length = 0·80 mm.) indicates that it was part of the dentition of a spalacotheriid distinctly smaller than *S. tricuspidens*. In themselves this difference in size and the temporal separation of the symmetrodonts found in the Paddockhurst Bone Bed and the Purbeck Beds do not warrant the establishment of a new species. Because there is an excellent chance that more material of this Wealden symmetrodont will be discovered, M21103 has not been assigned to a genus or species; only a comparison with *Spalacotherium tricuspidens* is suggested.

? Subclass THERIA Parker and Haswell 1897

Specimen M21104 (text-fig. 10). The crown of this small, trenchant premolariform tooth (length 0·85 mm., width 0·25 mm.) consists of a large, central cusp and smaller anterior and posterior accessory cusps. On one side of the crown there is a short ridge on the slope of the anterior accessory cusp and a longer but less distinct, cingulum-like expansion of the base of the crown on the posterior half of the central cusp. The two well-separated and divergent roots, which appear to be complete, have narrowly oval cross-sections; their length and disposition suggest that M21104 is a deciduous premolar.

Identification of M21104 poses a number of problems. Considering the roster of mammals that could be expected in an Early Cretaceous fauna only the representatives of one order, Multituberculata, lacked premolars grossly similar to M21104. In spite of

the lack of great morphologic differentiation, the premolars of other Late Jurassic and, presumably, Early Cretaceous mammals differ in a few minor characters that might be of taxonomic significance. The premolars of triconodonts have at least a lingual cingulum or a definite expansion of the lingual base of the crown. Anterior and posterior accessory and cingular cusps are common. The roots of the permanent premolars are close together, nearly parallel, and almost twice as long as the crown is high. The DP_4 of *Triconodon mordax*, the only triconodont deciduous premolar discovered so far, is molariform. It appears unlikely that M21104 is a triconodont premolar. Allocation to

a   b
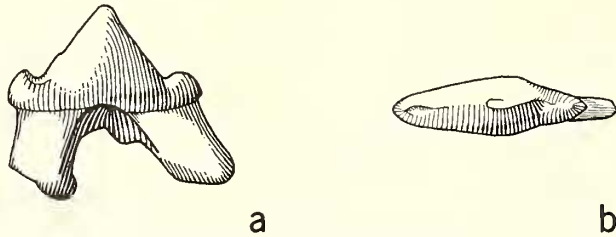
TEXT-FIG. 10. ? Therian, premolar, M21104, ×30. *a*, Lateral view; *b*, occlusal view.

the Order Docodonta also can be regarded as improbable for the premolars of *Docodon*, a Late Jurassic member of this order, have a distinct lingual cingulum and exhibit other differences in morphology. The premolars of many pantotherian species have a lingual cingulum, but in some species of eupantotheres—for example, note the upper premolars of *Amblotherium pusillum*—basal cingula are indistinct or absent. The Paddockhurst Bone Bed is high in the sequence of Wealden strata and mammals of eutherian–metatherian grade might have been present at the time it was deposited. M21104 is a type of premolar that might be expected in such a mammal. In summary, M21104 is certainly not a multituberculate premolar and probably not a triconodont or docodont premolar. Its allocation to the subclass Theria is based on both a process of elimination and the observation that the premolars of some Mesozoic therians lack a basal cingulum.

STRATIGRAPHY

Although no attempt will be made to describe the stratigraphy of the Cliff End and Paddockhurst Bone Beds in detail, a few comments are necessary in order to interpret the significance of the mammalian fossils.

Derived Upper Kimeridgian and basal Portlandian ammonites and other invertebrates were discovered by Allen (1960b) in the Top Lower Tunbridge Wells Pebble Bed. This would suggest that the Wealden mammalian fossils, especially those found in the coarse sands of the Cliff End Bone Bed, might have been derived from older deposits. The Ashdown Beds in which the Cliff End Bone Bed occurs have been interpreted by Allen (1959) as delta-face and shore-face deposits formed during a period of deltaic advance. As would be expected in a unit of this origin, the vertebrate fossils from the Cliff End Bone Bed are comminuted, rolled, and abraded. However, most of the specimens of derived Jurassic ammonites found in the Top Lower Tunbridge Wells Pebble Bed are internal casts of parts of a camera or one or two camerae, the largest being

approximately half a whorl (Arkell 1960); and all the derived invertebrates found in this pebble bed give evidence of transport and extended or intensive weathering. It is doubtful if the small mammalian fossils found in the Cliff End Bone Bed could have survived similar weathering and transport in addition to the fragmentation and abrasion involved in their concentration and deposition on the delta face. In contrast to the Ashdown Beds, the Grinstead Clay has been interpreted as a unit deposited during the lacustrine transgression of the Lower Tunbridge Wells delta (Allen 1959). The vertebrate fossils found in the Paddockhurst Bone Bed appear to be less fragmented and abraded than those found in the Cliff End Bone Bed, indicating that they too probably were not derived from older strata.

Additional evidence that the Cliff End mammals were not derived from Jurassic beds comes from a study of the animals themselves. The little that is known of the dentition of *Loxaulax valdensis* suggests that this species had a slightly more ptilodont-like dentition than the Purbeckian plagiaulacids. Assuming that the ptilodont multituberculates evolved from a plagiaulacid ancestor, the stage of evolution of *L. valdensis* suggests that the species is of post-Purbeckian age. The differences between the other Wealden mammals and their Purbeckian counterparts can also be interpreted as being indicative of a post-Purbeckian age. However, knowledge of the phylogeny of Mesozoic mammals is far from complete and any age-determination based on an assessment of the stages of evolution of these mammals can only be regarded as a suggestion. Finally, Allen (1960b) has determined that the derived Jurassic fossils found in the Top Lower Tunbridge Wells Pebble Bed were transported into the basin by a river flowing from the north. In contrast he found that the pebbles in the Cliff End Bone Bed were brought in from the north-east. Although the latter sediments contain glauconitic sand apparently derived from Jurassic strata, Upper Kimeridgian and basal Portlandian pebbles from the north-east are absent or rare. None of these lines of evidence conclusively demonstrates that the mammalian fossils found in the Wealden bone beds were not derived from older strata, but in concert they make this improbable.

Neither a precise determination of the stratigraphic position of the Cliff End Bone Bed within the Ashdown Beds nor an exact correlation of its time of deposition with the standard chronology based on the European marine sequence has been accomplished as yet. Currently the bulk of the Wealden of England is regarded as being of post-Tithonian age (Allen 1955, 1959, and Hughes 1958). Certainly the fossil localities are of pre-Aptian age. The differences between members of the Cliff End and Purbeck mammalian faunas suggest, but do not in themselves confirm, that the Cliff End Bone Bed is younger than the mammal-bearing strata of the Purbeck Beds. Hughes (1958), on paleobotanical evidence, allocates the Ashdown Beds to the Valanginian. Allen (1955, 1959) has correlated the period of deposition of the Ashdown Beds with the Berriasian regression. Thus a post-Purbeckian age is indicated for the Cliff End Bone Bed. The Paddockhurst Bone Bed is part of the Grinstead Clay, a unit stratigraphically higher than the Ashdown Beds. Using paleobotanical data, Hughes (1958) allocated the Tunbridge Wells Sandstone, which includes the Grinstead Clay, to the later Hauterivian. Allen (1959) suggested that the Grinstead Clay was deposited during a lacustrine transgression associated with later Valanginian or early Hauterivian changes in the level of the Neocomian sea in the Paris basin.

In summary, it appears that the Wealden mammalian fossils were not derived from

older strata. The mammalian fauna of the Cliff End Bone Bed is probably of early Neocomian age, whereas that of the Paddockhurst Bone Bed is distinctly younger. Both faunas are post-Purbeckian and pre-Aptian in age.

CONCLUSION

The discovery of these few Wealden fossils has increased knowledge of the morphology of the plagiaulacid multituberculate *Loxaulax valdensis*; extended the demonstrated range of the Eupantotheria, previously limited to the Middle and Late Jurassic; and established the presence of the Symmetrodonta in England in the Early Cretaceous. The mammalian fauna of the Cliff End Bone Bed, which is part of the Ashdown Beds, consists of *L. valdensis* and a dryolestid eupantothere; the fauna of the younger Paddockhurst Bone Bed includes a spalacotheriid symmetrodont and possibly another therian and a plagiaulacid. These discoveries indicate that with proper collecting techniques more mammalian fossils probably can be obtained from these and other Wealden bone beds.

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